Sensitivity of secondary production and export flux to choice of trophic transfer formulation in marine ecosystem models

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Abstract. The performance of four contemporary formulations describing trophic transfer, which have strongly contrasting assumptions as regards the way that consumer growth is calculated as a function of food C:N ratio and in the fate of non-limiting substrates, was compared in two settings: a simple steady-state ecosystem model and a 3D biogeochemical general circulation model. Considerable variation was seen in predictions for primary production, transfer to higher trophic levels and export to the ocean interior. The physiological basis of the various assumptions underpinning the chosen formulations is open to question. Assumptions include Liebig-style limitation of growth, strict homeostasis in zooplankton biomass, and whether excess C and N are released by voiding in faecal pellets or via respiration/excretion post-absorption by the gut. Deciding upon the most appropriate means of formulating trophic transfer is not straightforward because, despite advances in ecological stoichiometry, the physiological mechanisms underlying these phenomena remain

incompletely understood. Nevertheless, worrying inconsistencies are evident in the way in which fundamental transfer processes are justified and parameterised in the current generation of marine ecosystem models, manifested in the resulting simulations of ocean biogeochemistry. Our work highlights the need for modellers to revisit and appraise the equations and parameter values used to describe trophic transfer in marine ecosystem models.

1. Introduction

Zooplankton are key players in the biogeochemical cycling of carbon and nutrients in marine ecosystems, especially in their roles in linking primary producers to higher trophic levels including fish (Beaugrand and Kirby, 2010; Beaugrand et al., 2010) and in the export of organic matter to the deep ocean (e.g., González et al., 2009; Juul-Pedersen et al., 2010). Parameterising zooplankton in models is however far from straightforward (Carlotti and Poggiale, 2010). Quantifying prey selectivity and ingestion is an important starting point given the role of zooplankton in top-down control of biomass stocks and so the functional response has received considerable attention (Gentleman et al., 2003; Mitra and Flynn, 2006). Once ingested, food items are used for growth, with associated losses via faecal material and respiration/excretion. The role of food quality in trophic transfer provides an additional dimension which has been the subject of numerous experimental studies that have investigated the roles of nutrient elements (Jones et al., 2002; Augustin and Boersma, 2006; Siuda and Dam, 2010) and biochemicals such as essential fatty acids (Mayor et al., 2009a; Burns et al., 2011) as factors limiting growth and reproduction. Food quality may interact with food quantity (in terms of carbon), yet C may often be in stoichiometric excess when present in the food of herbivorous zooplankton to the extent that "leftover C" must be disposed of via faecal material or increased metabolic activity and respiration (Hessen and

Anderson, 2008). These pathways for disposal have important implications for C cycling and C use efficiency of food webs as a whole (Hessen et al., 2004).

The theoretical basis of ecological stoichiometry has advanced considerably in recent years. Early models, with zooplankton as their focus, examined the potential for limitation by carbon versus nutrient elements, usually assuming that the latter can be used for growth with high efficiency whereas C is necessarily consumed in maintenance. Elemental ratios in grazer and food are used to calculate threshold elemental ratios (TERs) that, by definition, are the crossover from limitation by one element to another (Anderson, 1992; Hessen, 1992). In freshwater systems, phosphorus was identified as the element limiting the production of zooplankton, notably cladocerans, whereas nitrogen was generally believed to be limiting in marine systems (Elser and Hassett, 1994). A case can, however, be made for limitation by carbon if the energy requirements for maintenance are sufficiently high (Anderson and Hessen, 1995). Since these early models, stoichiometric theory has been extended to include biochemical compounds (Anderson and Pond, 2000), improved representation of bioenergetic costs such as protein synthesis and turnover (Anderson et al., 2005), analysis of maternal biomass (in addition to food) as a source of nutrition (Mayor et al., 2009b), and Dynamic Energy Budget approaches for describing how competing substrates are utilised subsequent to absorption by the gut (Kuijper et al., 2004). As well as considering how food quality impacts on zooplankton growth, stoichiometric models for use in ecosystem scenarios also need to consider the fate of nonlimiting elements. The main choice to make in this regard is whether elimination of substrates in stoichiometric excess occurs pre- or post-absorption by the gut. In the former case (e.g., DeMott et al., 1998), excess substrates are packaged within faecal material which may sink out of the euphotic zone and thereby contribute to export flux to the deep ocean. Conversely, post-absorptive regulation (e.g., Anderson et al, 2005) favours recycling in dissolved form.

In the past, most marine ecosystem models, and particularly those running in general circulation models (GCMs), employed a single base currency (usually N or P) and, when necessary, converted to other currencies (notably C) by applying the Redfield ratio (e.g., Six and Maier-Reimer, 1996; Yamanaka and Tajika, 1997; Slagstad and Wassmann, 2001). With the realisation that many processes in marine food webs do not strictly conform to this ratio (especially for carbon versus nutrient elements, e.g., Anderson and Pondaven, 2003), models today often employ non-Redfield stoichiometry. For example, whereas a C:N ratio of 6.625 (Redfield) may be assigned to phytoplankton, alternate values are more appropriate for other state variables such as zooplankton, bacteria and the detritus. Appropriate parameterisations are then required to describe trophic transfer that take into consideration stoichiometric imbalances between predator and prey and how substrates in excess are dealt with. A wide range of such parameterisations is used in contemporary marine ecosystem models, begging the question as to whether predicted biogeochemical cycling is sensitive to this choice and, if so, the extent to which different choices can be justified in context of the experimental/observational literature.

Here, we compare the performance of four different trophic transfer formulations within two settings: (1) a simple steady-state ecosystem model, and (2) a 3D biogeochemical GCM (Yool et al., 2011). The four trophic transfer schemes are taken from: AH95 (Anderson and Hessen, 1995), ERSEM (European Regional Seas Ecosystem Model: Blackford et al., 2004), HadOCC (Hadley Centre Ocean Carbon Cycle model: Palmer and Totterdell, 2001) and Pah08 (Pahlow et al., 2008). The latter three are ecosystem models while the first, AH95, is the trophic transfer scheme used in the recently published MEDUSA (Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification) ecosystem model (Yool et al., 2011). Each has thus been implemented within ecosystem models and, as such, may be considered to be representative of the current state-of-the-art in this field. There is

considerable variation in the assumptions underpinning the chosen transfer schemes (section 2) and, as a consequence, in the resulting predictions of transfer to higher trophic levels and carbon export (sections 3, 4). Our aim is to highlight these differences and discuss them in context of the existing observational/experimental literature and the need for reliable parameterisations of non-Redfield stoichiometry in the next generation of marine ecosystem models.

2. Trophic transfer schemes

The metabolic budget of organisms, including different anabolic and metabolic requirements and how these are met from available substrates, needs to be taken into consideration when constructing trophic transfer formulations for use in ecosystem models. Rules are required to govern the absorption of ingested substrates across the gut, limitation of growth in the face of variable elemental composition in food with associated losses via respiration and excretion, and for how remaining substrates in stoichiometric excess are dealt with. In this respect, the four trophic transfer formulations studied here, AH95, ERSEM, HadOCC and Pah08, vary markedly in their assumptions (Figure 1). Note that basal metabolic costs are not met directly using ingested substrates in any of these formulations but rather, when implemented in ecosystem models, a biomass-specific term is included as an additional loss rate. Within other, more recent, trophic transfer schemes (Anderson et al, 2005; Mitra 2006; Acheampong et al., 2012) ingested food is first and foremost allocated to basal metabolism, taking priority over other functions including growth. We considered including these formulations in the analysis here but, due to the radically different way that basal metabolism is represented, chose not to do so because it is difficult to achieve a fair comparison. Also, none of the four constructs used here consider the more complex issues of food quality and quantity discussed by Mitra and Flynn (2005, 2007) and Flynn (2009).

Although undoubtedly important, the aim here is specifically to consider simpler model structures currently in use in marine ecosystem models, to illustrate how even minor differences can have significant impacts on the overall simulation. Our focus is thus on investigating model sensitivity to assumptions regarding how growth is limited by food quality (C:N) and for the fate of substrates in excess.

The four trophic transfer schemes (Figure 1) were initially set up using published parameter values. The objective is to compare functional forms and associated assumptions and so parameter values were adjusted, as far as possible, to be consistent with each other while remaining as faithful as possible to the originals. A fixed molar C:N for zooplankton, θ_Z, of 5.5 (Gismervik, 1997) was set in each case, whereas food C:N, θ_f, was allowed to vary. Two changes to the published parameterisations were then made. First, excluding material voided as stoichiometric excess, all formulations were assigned a fixed absorption efficiency (AE) for N of 0.7 (e.g., Palmer and Totterdell, 2001, Blackford et al., 2004). Note that absorption efficiency is more commonly, but incorrectly, known as assimilation efficiency (assimilation is anabolism, the incorporation of absorbed digestive products into organismal tissue: Penry, 1998). For simplicity, carbon absorption efficiency was also set to 0.7, otherwise additional rules would be required in some cases in order to deal with the imbalance. Second, with a C:N ratio of 6.625 (the Redfield ratio) for θ_f, parameter values were adjusted to achieve a gross growth efficiency (GGE) for N of 0.5, which is close to the average of predicted efficiencies of 0.25, 0.5, 0.7, and 0.6 for the AH95, ERSEM, HadOCC and Pah08 formulations respectively (after assigning fixed AE of 0.7). Bearing in mind these alterations, summary descriptions of the four trophic transfer schemes are as follows:

AH95: Stoichiometric regulation of homoeostasis in zooplankton biomass occurs post-absorption by the gut. After first calculating losses to faecal pellets from absorption efficiencies, either C or N in remaining substrates limits growth depending on specified

maximum net production efficiencies, k_C^* and k_N^*, of 0.3 and 1.0 respectively (in the case of C, 1-k_C^* is respired). If C and N are absorbed with equal efficiencies, the threshold elemental ratio (TER) occurs at $\theta_Z k_N^* / k_C^*$, i.e., the ideal food C:N is >> θ_Z. The limiting element is utilised with maximum net production efficiency, with excess C or N respired or excreted in inorganic form. A complication is that absorption is calculated not in terms of C and N, but rather nitrogenous compounds (proteins, assumed to have a fixed C:N of 3.96 and AE of 0.68) and non-nitrogenous compounds (C only; AE=0.49). This absorption scheme was replaced here with fixed AEs for C and N of 0.7, as was also the case when the AH95 trophic transfer formulation was implemented in ecosystem models by Anderson and Pondaven (2003) and Yool et al., (2011). In order to achieve GGE for N of 0.5 (for θ_f = 6.625), maximum zooplankton net production efficiency for C was increased from 0.3 to 0.593.

ERSEM. Unlike AH95, losses to faecal material are not deducted prior to calculating growth. The ideal θ_f equals the body composition of the consumer such that C limits if $\theta_f < \theta_Z$ and N limits if $\theta_f > \theta_Z$. The limiting element is used with a fixed gross growth efficiency, K, of 0.5. Fraction 1-K is allocated according to parameters eu (0.9) and pdom (0.333), with 1-eu as inorganic release (respiration of C or excretion of N), eu(1-pdom) as faecal material and eu.pdom as dissolved organic matter (DOM). The resulting absorption efficiency for the limiting element is 1-(eu(1-pdom)) = 0.7. Equivalent fluxes are calculated for the non-limiting element, proportional to θ_Z. Remaining C or N in stoichiometric excess is either allocated to faecal pellets in the case of C, or excreted as inorganic N. Note that the ecosystem models we use here do not include DOM, so the fluxes to DOM are instead assigned to inorganic nutrient and CO_2.

HadOCC. As for ERSEM, the ideal θ_f equals θ_Z. The limiting element is used with K = 0.7 with the remainder, 1-K, potentially allocated to detritus although there is a complication in

that detritus is assumed to have a fixed C:N ratio, θ_D, of 7.5. An imbalance occurs if this ratio differs from the C:N of the consumer, in which case as much as possible of the C and N is allocated to detritus with the rest released as inorganic nutrient or CO_2. Finally, excess C or N resulting from θ_f being unequal to θ_Z is similarly released as inorganic nutrient or CO_2. For the purposes of the comparison here, parameter K was decreased from 0.7 to 0.5.

Pah08. Again, ideal food C:N equals θ_Z, but this time with K = 0.9. C and N not assimilated into biomass, including excesses accruing from predator-prey stoichiometric imbalance, are allocated between DOM (fraction f_x^d) and egestion as faeces (1- f_x^d), where parameter f_x^d has a value of 0.25. Absorption efficiency is thus 0.925 when consuming ideal prey, decreasing as excess C or N are present in the diet. In order to be consistent with the other transfer schemes, parameter f_x^d was increased to 0.4 and K altered to 0.5 in order to give AE of 0.7 for ideal prey. As for ERSEM, fluxes to DOM were allocated to inorganic pools in the ecosystem models studied here.

It is worth noting that it was by no means trivial to set up the trophic transfer schemes by reading the published literature. In some instances, we contacted the original authors to ensure that our interpretation of their equations was correct. For the interested reader, we have put together an Excel spreadsheet in which each of the four formulations is set up in turn. This is available on request from the first author.

The predicted allocation of N and C between growth, excretion/respiration and faecal pellets, for each of the four trophic transfer schemes, is shown in Figure 2 for θ_f between 4 and 20. The first point to note is that the ERSEM, HadOCC and Pah08 formulations all give identical predictions for GGEs for both N and C because they each assume that optimum θ_f (the TER) equals θ_Z and then use a fixed GGE (0.5) for the limiting nutrient. Thus, N GGE is 0.5 for $\theta_f \geq 5.5$ (N limitation), whereas it reaches a value of 0.7 for $\theta_f \geq 9.27$ in AH95 (the

198 formulations were all parameterised to give N GGE = 0.5 for θ_f = 6.625). Excess N at a low
199 θ_f is excreted in inorganic form in all models, although in Pah08 a fraction of this N is also
200 allocated to faecal material. Significant remineralisation of inorganic N occurs for all θ_f in
201 ERSEM and Pah08, but goes to zero in AH95 and HadOCC as absorbed substrates are used
202 for growth with 100% efficiency. The HadOCC formulation allocates significantly more N to
203 faecal pellets for $\theta_f \geq 7.5$ as compared to the other trophic transfer schemes, 0.5 versus 0.3.
204 The patterns for allocation of C to respiration and faecal pellets are even more disparate.
205 AH95 and ERSEM represent opposite ends of the spectrum, with excess C being respired in
206 the former and allocated to faecal pellets in the latter. Pah08 is in between. The HadOCC
207 formulation is constrained by the need to maintain a fixed C:N in detritus (7.5) such that, at
208 high θ_f, most C in food is respired. Overall, it is worth noting the strong asymmetry in
209 allocation schemes for C and N, and how this asymmetry varies between the different trophic
210 transfer formulations.

211 Predicted GGEs for N and C are compared in Figure 3 with experimental data (Kiørboe,
212 1989) in which egg-producting female *Acartia tonsa* were fed the diatom *Thalassiosira*
213 *weissflogii* with C: N ratios manipulated via nutrient concentrations in the algal medium
214 (similar experimental results were found by Checkley (1980) for the copepod *Paracalanus*
215 *parvus*). The decline in C GGE with increasing phytoplankton C:N predicted by the ERSEM
216 trophic transfer formulation (and thereby also HadOCC and Pah08 which give the same
217 result) shows good agreement with the data, a result of increasing severity of N limitation.
218 The same trend is seen with the AH95 formulation, although it is slightly elevated relative to
219 the data. In the case of N, the constant N GGE of 0.5 (except at low θ_f) predicted by the
220 ERSEM formulation lies slightly above the data, but is not unreasonable. The AH95
221 formulation, in contrast, predicts considerably higher N GGE. It would be harsh, however, to

hastily condemn this model-data mismatch because it is hard to explain the low and more or less constant N GGE of ~0.4 seen in the data. One might expect N to be utilised for growth with high efficiency when it is limiting in the diet. Given typical AE for N of 0.6-0.9 (Hassett and Landry, 1988; Anderson, 1994), why are zooplankton apparently so wasteful in using it for growth? Maintenance costs, such as protein turnover, could be involved (e.g. Boersma and Kreutzer, 2002; Mayor et al., 2011), but it is as yet unclear as to whether these are sufficient in magnitude to significantly impact on overall growth efficiency.

3. Steady state model

3.1. Model description

A simple steady state ecosystem model of the euphotic zone was constructed in which each of the four trophic transfer schemes was implemented in turn. The transparency provided by the simplicity of the food web structure and associated parameterisation (other than trophic transfer, there are very few parameters) is justified in that the model is easy to understand and analyse. A purely theoretical approach is therefore appropriate in this instance (there is no attempt to compare with field data), although results will be discussed with reference to the results obtained using the 3D global GCM (section 4). As far as possible, the steady state and 3D models were made to be consistent in terms of ecosystem structure and parameterisation.

The food web model, which has both C and N as currencies, traces flows only, with no representation of stocks (Figure 4). Separation at pathway junctions is specified by linear parameterisations, permitting analytic solutions, which are presented for different values of phytoplankton C:N ratio (θ_P), to be readily obtained. The starting point of the model is new production (nitrate uptake) by phytoplankton (P), P_n, against which subsequent flows within the food web are normalised. Carbon uptake associated with new production is $\theta_P P_n$. New

247 production is supplemented by regenerated production, P_r, accrued from ammonium (A)
248 regenerated within the food web. The grazer community in the model is separated into two
249 types: herbivores (H), which graze P, and an infinite chain of carnivores (Z). Zooplankton are
250 often relatively homeostatic with respect to their biochemical composition (Andersen and
251 Hessen 1991) and so H and Z were assigned fixed C:N ratios, θ_H and θ_Z respectively, of 5.5
252 (e.g., Gismervik, 1997). Two types of detritus are distinguished in the model, slow- and fast-
253 sinking (D_1 and D_2, respectively), in similar fashion to other marine ecosystem models
254 (Leonard et al., 1999; Salihoglu et al., 2008; Yool et al., 2011). The former, which is largely
255 remineralised in the upper water column, is in the model derived from non-grazing
256 phytoplankton mortality (see below) and faecal pellet production by herbivores. Fast sinking
257 detritus results from carnivore faecal pellets. Given that the model is steady state, detritus
258 exported from the euphotic zone necessarily equals P_n.

259 Grazing usually dominates phytoplankton losses in marine ecosystems (Banse, 1994)
260 although other factors such as viral lysis may sometimes be important (Bratbak et al., 1990;
261 Thingstad, 2000). While faecal pellets may constitute a large part of the vertical flux to the
262 deep ocean (e.g., Honjo and Roman, 1978), material may also be exported in the form of
263 decaying phytoplankton as marine snow (Lampitt et al., 1993). The relative contribution of
264 pellet material to export remains incompletely understood (Turner, 2002). In the model, 68%
265 of primary production is assumed to be grazed (parameter $\gamma = 0.68$), this being the average
266 obtained from the base run of the 3D GCM (section 4). Similar values, 70%, 73% and 67%
267 were obtained using biogeochemical ocean GCMs by Sarmiento et al (1993), Schmittner et
268 al. (2005) and Yool et al. (2011) respectively. The remaining non-grazing mortality, 1-γ, is
269 allocated directly to D_1. Starting with the herbivores, a fixed fraction, ϕ, of ingested material
270 is lost to ammonium. Parameter ϕ takes account of two processes. First, there is “messy

feeding", accounting for 20% of ingestion (Yool et al., 2011). Second, a fraction of intake is allocated to meet the cost of basal metabolism. This is often specified as a biomass-specific loss term in models but, as the steady state model does not include stocks, it is here related to intake. If biomass-specific basal metabolism is 2% d^{-1} (Yool et al., 2011), intake is 1.0 d^{-1} and growth efficiency is 0.5, then 4% of intake is required (ideally, basal metabolic costs could be deducted post-absorption, but for simplicity this is not the case here). Thus, $\phi = 0.20 + 0.04 = 0.24$. In the case of N, remaining ingested material is processed with a fixed absorption efficiency, β_{HN}, with the remainder $(1-\beta_{HN})$ lost as faecal material to detritus (D_1). The absorbed substrates are then used for growth with a fixed net production efficiency, k_{HN}, with $(1-k_{HN})$ excreted as ammonium. Following the same principles, β_{ZN} and k_{ZN} quantify trophic transfer of N by carnivorous zooplankton, and commensurate C flows are specified by β_{HC} and k_{HC} (herbivores) and β_{ZC} and k_{ZC} (carnivores). Values for the β_i and k_i parameters are taken from the allocations to C and N as a function of θ_f as shown in Figure 2. Detritus (sinking particles) is either exported from the euphotic zone, fractions ζ_1 and ζ_2 for slow- and fast-sinking respectively, or remineralised as ammonium. Parameters ζ_1 and ζ_2 were assigned values from the base run of the 3D model (section 4), giving $\zeta_1 = 0.27$ and $\zeta_2 = 0.68$.

An advantage of using a simple linear approach to parameterisation is that it is straightforward to provide equations that describe the steady state solution of the model. Production by herbivores, G_H, is:

$$G_H = \gamma(1-\phi)\beta_{HN}k_{HN}(P_n+P_r) \quad (1)$$

The associated export flux via D_1, $Ex_{D1(N)}$, needs to take into consideration the fraction of phytoplankton lost to non-grazing mortality, $1-\gamma$, and the fact that only fraction ζ_1 of D_1 produced is exported:

$$Ex_{D1(N)} = \zeta_1((1-\gamma) + \gamma(1-\phi)(1-\beta_{HN}))(P_n+P_r) \quad (2)$$

The equivalent terms for production of carnivores and associated export via D_2, G_Z and $Ex_{D2(N)}$, are calculated on the basis that carnivores are ordered into an infinite chain:

$$G_Z = G_H \sum_{i=1}^{\infty} ((1-\phi)\beta_{ZN}k_{ZN})^i = G_H(f[(1-\phi)\beta_{ZN}k_{ZN}]-1) \quad (3)$$

$$Ex_{D2(N)} = \zeta_2 G_H(1-\phi)(1-\beta_{ZN}) \sum_{i=0}^{\infty} ((1-\phi)\beta_{ZN}k_{ZN})^i$$

$$= \zeta_2 G_H(1-\phi)(1-\beta_{ZN}) f[(1-\phi)\beta_{ZN}k_{ZN}] \quad (4)$$

where function f[x] is:

$$f[x] = \sum_{i=0}^{\infty} x^i = 1/(1-x),\ 0 < x < 1 \quad (5)$$

Corresponding terms for export of C, $Ex_{D1(C)}$ and $Ex_{D2(C)}$, are:

$$Ex_{D1(C)} = \zeta_1((1-\gamma) + \gamma(1-\phi)(1-\beta_{HC}))\theta_P(P_n+P_r) \quad (6)$$

$$Ex_{D2(C)} = \zeta_2\theta_H G_H(1-\phi)(1-\beta_{ZC}) f[(1-\phi)\beta_{ZC}k_{ZC}] \quad (7)$$

All that remains is to calculate regenerated production, P_r. The fate of nitrogen (nitrate or ammonium) consumed in primary production is either to be exported and lost from the system, or recycled to the ammonium pool from where it starts its journey round the food web again. The probability of the latter, p_A, is:

$$p_A = 1 - (Ex_{D1(N)}+Ex_{D2(N)})/(P_n+P_r) \quad (8)$$

Replacing the terms in the above equation with those in Eqs. (1), (2) and (4), and rearranging, gives:

$$p_A = 1 - \zeta_1((1-\gamma)+\gamma(1-\phi)(1-\beta_{HN})) - \zeta_2\gamma(1-\phi)\beta_{HN}k_{HN}(1-\phi)(1-\beta_{ZN}) f[(1-\phi)\beta_{ZN}k_{ZN}] \quad (9)$$

P_r is then calculated by taking into account repeated recycling of N by the food web:

$$P_r = P_n[p_A + p_A^2 + p_A^3 + p_A^4 + \ldots] = P_n(f[p_A]-1) \quad (10)$$

3.2. Results

317 Results are presented showing how predicted nutrient cycling and export relate to
318 phytoplankton C:N ratio. While the canonical Redfield ratio may be representative of
319 autotroph cell growth under optimum conditions (Geider and La Roche, 2002; Finkel et al.,
320 2010), it is known that phytoplankton C:N can strongly differ from Redfield (e.g., Daly et al.,
321 1999; Sterner et al., 2008; Flynn, 2010). Values double or treble the Redfield ratio can occur
322 in response to high light and/or low nutrient conditions (Dickman et al., 2006; Hessen et al.,
323 2008). It is also worth noting that phytoplankton at times make up a modest fraction of seston
324 (Frigstad et al., 2011) and when zooplankton feed on seston of mixed origin they may face
325 major deviations in food stoichiometry. We chose to analyse model solutions for θ_P between
326 4 and 20.

327 Results of the steady state model are shown in Figure 5, in all cases normalised against
328 external N input to the system (i.e., P_n=1). Primary production drives the food web and, new
329 and regenerated production summed together, reaches 4 to 6 and is thus dominated by P_r (Fig.
330 5a). Equivalent *f*-ratios are ~0.15 to 0.25, similar to those estimated for ocean systems
331 (Eppley and Peterson, 1979). Three sources of recycling of N contribute to regenerated
332 production in the model: direct release by grazers via messy feeding and basal metabolism
333 (parameter ϕ), excretion by grazers (1-k_N) and remineralisation of detritus (1-ζ), accounting
334 for approx. 30-40%, 20-30% and 40-50% of ammonium release respectively (except for the
335 HadOCC version where excretion by grazers and remineralisation of detritus levelled off at
336 6% and 60% respectively at high θ_P). Of the detritus produced, approx. 45% is from non-
337 grazing phytoplankton mortality, with the remainder as faecal pellets. The variation seen in
338 total primary production is mainly due to the excretion term such that the ERSEM and Pah08
339 model versions predict the highest primary production at high θ_P because these two
340 formulations exhibit significant excretion even when N is limiting production (Fig. 2a). All

models show increasing primary production when herbivores are limited by C (low θ_P, less than the TER) as herbivores excrete the non-limiting element, N, which is in excess.

Herbivore production, which depends jointly on N GGE and total primary production (Eq. 1), shows considerable variation between the different model versions (Fig. 5b). It increases with increasing θ_P under C-limiting conditions (θ_P < TER) as N is progressively used with greater efficiency and excretion of excess N diminishes. At high θ_P, the greatest N GGE is associated with the AH95 trophic transfer formulation (Fig. 2a), giving rise to the highest predicted G_H of 1.72. In contrast, herbivore production is only 1.10 when using the HadOCC model version, lower than 1.34 for ERSEM and Pah08, but not because of lower N GGE (these three trophic transfer formulations give rise to the same N GGE: Fig. 2a), but rather because it has the lowest primary production (Fig. 5a). In the case of carnivores, there is no direct influence of θ_P on G_Z but, rather, G_Z depends on G_H and GGE (Eq. 3). Thus, the trends seen in carnivore production mirror those for herbivores (Fig. 5c) although the ERSEM model version exhibits higher production than AH95 because the N GGE for θ_f = 5.5 (the C:N of prey) is higher (0.5 vs. 0.42).

As for secondary production, large differences in predicted export are seen when using the different trophic transfer formulations. Total carbon export, and its variation with θ_P, is dominated by the slow-sinking fraction (Fig. 5d, f), emphasising the importance of correctly parameterising herbivore stoichiometry and associated trophic transfer in models. Greatest carbon export is associated with the ERSEM and Pah08 model versions as excess C generated at high θ_P is allocated to herbivore faecal pellets, whereas in the other versions some or all of the excess C is respired to CO_2. It is interesting to note how predicted C export is decoupled from the trophic transfer of N. Unlike the export of N which is constrained in that $Ex_{D1(N)} + Ex_{D2(N)} = P_n$, the same is not true for C, i.e., $Ex_{D1(C)} + Ex_{D2(C)}$ does not

necessarily equal $\theta_P P_n$. In fact, this result is not surprising as *pe*-ratio (export of organic carbon/primary production: Dunne et al., 2005) only equals *f*-ratio (in steady state) if there are no stoichiometric imbalances in the system. If the C:N of detritus exceeds that of phytoplankton, which may be expected if C absorption efficiency is less than that for nutrient elements (e.g., Mayor et al., 2011), then C export will exceed that fixed in new production, $\theta_P P_n$. The C:N ratio of exported detritus does indeed exceed that of phytoplankton in the model predictions derived using the ERSEM trophic transfer formulation (except for $\theta_P = 5.5$, when the two are equal) due to allocation of excess C to faecal pellets. It is perhaps more surprising that, at high θ_P, the C:N ratio of export is lower than θ_P when using the AH95 and HadOCC trophic transfer formulations, a result of excess C being respired to CO_2. The C:N of particulate organic matter is remarkably constant in the marine systems (Chen et al, 1996), close to the Redfield ratio. If excess C in phytoplankton is respired to CO_2 this may, to some extent, buffer the system against variability in phytoplankton C:N.

Although fast-sinking detritus represents only a minor fraction of the total export, parameterising it accurately in models is important because it reaches great depths. Unlike D_1, the C:N ratio of this fraction is not directly related to θ_P but is instead proportional to herbivore production, G_H (Fig. 5e). It therefore shows the same trends as G_Z versus θ_P (Fig. 5c), although inverted in terms of magnitude (HadOCC highest, ERSEM lowest). Thus, herbivores dampen the system by ironing out stoichiometric imbalances associated with phytoplankton C:N, but parameterisation of carnivores is also important because this determines the proportionality between G_H and export of D_2.

4. 3D General circulation model

4.1. Methodology

A new ecosystem model, MEDUSA-1.0 (Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification; henceforth MEDUSA) was recently used in a multi-decadal hindcast simulation in the NEMO (Nucleus for European Modelling of the Ocean) global GCM (Yool et al., 2011). We compare the performance of the different trophic transfer formulations in this biogeochemical GCM, after making modifications to the parameterisation of trophic transfer in MEDUSA to provide consistency with the steady-state model.

MEDUSA is an intermediate complexity ecosystem model, specifically designed for the global domain, which divides the food web into "small" and "large" portions (Fig. 6). Size structure may be expected to affect the relationship between primary production, secondary production and export, with greater transfer of carbon to higher trophic levels in systems dominated by large organisms ordered in short food chains (Michaels and Silver, 1988). Nanophytoplankton and microzooplankton dominate the small fraction, together with slow-sinking detritus particles. The large portion includes diatoms and mesozooplankton, together with large detritus particles that are afforded an implicit representation because of their fast sinking rate. Phytoplankton chlorophyll is explicitly represented, permitting photoacclimation of C:chl in response to ambient light. Nitrogen is the base currency of the model, with the biogeochemical cycles of silicon and iron also included. Slow sinking detritus is produced via mortality of non-diatom phytoplankton and microzooplankton faecal pellets. It sinks at a speed of 3 m d^{-1} and is subject to both remineralisation and grazing by micro- and mesozooplankton. Fast sinking detritus is derived from mortality of diatoms and faecal pellet production by mesozooplankton. It is not modelled explicitly but rather, at each time step, production of large particles is instantly remineralised through the vertical levels of the model based on the ballast theory of Armstrong et al. (2002). For a full description of MEDUSA, including a comprehensive list of equations and parameter values, see Yool et al. (2011).

The trophic transfer scheme used in MEDUSA, as published in Yool et al (2011), is AH95, including fixed absorption efficiencies for C and N. Although C is not explicitly represented as a model currency, phytoplankton and zooplankton are assigned (fixed) C: N ratios for the purpose of calculating trophic transfer (the model run described in Yool et al. (2011) assigned the Redfield ratio of 6.625 to each). Other associated parameter values used by Yool et al. (2011) are $\beta_N = \beta_C = 0.69$ (Anderson, 1994) and $k_C = 0.80$ (Anderson and Pondaven, 2003). For the purpose of intercomparison of the trophic transfer schemes, and to provide consistency with the steady state model, these parameters were reassigned values as for AH95 (section 2), i.e. $\beta_N = \beta_C = 0.70$, $k_C = 0.593$ and $\theta_Z = 5.5$. In addition to these changes in model parameter values, one alteration was made to the formulation of grazing in order to provide consistency with the steady-state model. In MEDUSA, as published in Yool et al. (2011), microzooplankton graze on non-diatoms and slow sinking detritus while mesozooplankton consume non-diatoms, diatoms, microzooplankton and slow-sinking detritus. As there was no grazing by zooplankton on detritus in the steady state model, we therefore reconfigured the flow pathways in MEDUSA to remove grazing on detritus, maintaining proportionality in prey preference parameters for remaining prey items (Fig. 6). Furthermore, MEDUSA does not have a state variable for detritus C. Trophic transfer and associated ecosystem dynamics are not compromised by this omission as there is no feedback between detritus C and ecosystem functioning. Model predictions for export are therefore quantified, and compared for the different trophic transfer formulations, in N units.

Running a global biogeochemical GCM is a computationally intensive exercise and so, whereas model solutions for a wide range of phytoplankton C:N ratios were investigated with the steady-state model, the 3D study investigated only $\theta_P = 6.625$ (the Redfield ratio). Microzooplankton feed solely on phytoplankton in the model and are therefore exposed only to $\theta_f = 6.625$. Mesozooplankton, on the other hand, graze on a mixture of both phytoplankton

and microzooplankton and so food quality is variable, $5.5 \leq \theta_f \leq 6.625$. The model ecosystem is driven by N and so it is the difference in N allocation schemes (Fig. 2a; values for θ_f = 5.5, 6.625 listed in Table 1) that is significant for simulated ecosystem dynamics. In this regard, the ERSEM and Pah08 trophic transfer formulations are exactly equivalent for this range of food C:N and so the work therefore involves a 3-way comparison where MEDUSA (incorporating AH95) is compared with simulations in which the AH95 trophic transfer scheme is replaced in turn by ERSEM/Pah08 and HadOCC (parameterised as in section 2). Points to note from Table 1 are: (1) N GGE for θ_f = 6.625 is the same (0.5) for all the transfer schemes; (2) AH95 and ERSEM are identical for θ_f = 6.625, but differ for θ_f = 5.5 (microzooplankton as prey) with lower growth efficiency (0.42 vs. 0.5) and higher nutrient regeneration (0.28 vs. 0.2) in AH95; (3) allocation to faecal pellets is highest, and excretion of nutrient lowest, with the HadOCC trophic transfer formulation and, furthermore, this occurs for both θ_f = 5.5, 6.625 (and thus will come into play when both microzooplankton and phytoplankton are prey items).

The physical GCM used (for details, see Yool et al., 2011) is version 3.2 of NEMO (Madec, 2008), configured at approximately 1º x 1º resolution, higher around the equator to improve the representation of equatorial upwelling. There are 64 levels in the vertical, increasing in thickness from approximately 6 m at the surface to 250 m at 6000 m. In order to improve the representation of deep water circulation, partial level thicknesses are used in the specification of bottom topography. Vertical mixing is parameterised from the turbulent kinetic energy (TKE) scheme of Gaspar et al. (1990), with modifications by Madec (2008). Sea-ice is simulated using the LIM2 sea-ice submodel, coupled to the ocean every 5 ocean time steps through the non-linear quadratic drag law of the shear between sea-ice and ocean surface velocity (Timmermann et al., 2005). Temperature and salinity fields are initialised

463 from a monthly climatology, with surface fields of the latter relaxed toward the climatology
464 throughout the simulation in order to prevent unacceptable drifts in salinity caused by
465 deficiencies in freshwater forcing.

466 Given that the MEDUSA ecosystem model was reconfigured (above), a new spinup of the
467 GCM was required. As for Yool et al. (2011), this spinup was a 40 year simulation, 1966-
468 2005, forced at the ocean surface with precipitation, downward short- and long-wave
469 radiation and winds from DFS4.1 fields developed by the European DRAKKAR
470 collaboration (DRAKKAR Group, 2007). The last 12 years of the spinup was then repeated
471 twice, but implementing the ERSEM and HadOCC trophic transfer schemes.

472 *4.2. Results*

473 Results as presented are averages of the last four years of each of the three simulations
474 (Fig. 7). For completeness, we also compare with biogeochemical fields predicted by
475 MEDUSA-NEMO as published by Yool et al. (2011) in Table 2. Yool et al. (2011) concluded
476 that their simulated patterns of nutrients and productivity were consistent with observations,
477 including major features such as the oligotrophic gyres and plankton blooms at high latitudes.
478 The new base run, using the reparameterised AH95 trophic transfer scheme (lower GGE),
479 gave rise to qualitatively similar patterns of biogeochemical tracers as in Yool et al (2011).
480 Quantitatively, primary production of 52.7 Gt C yr^{-1} is 15% higher in the new run due to
481 increased nutrient recycling by zooplankton but, as it happens, the Yool et al. (2011) value of
482 45.7 Gt C yr^{-1} is on low end of estimates based on satellite-based chlorophyll and the new
483 value is still lower than estimates of 58.8 and 60.4 Gt C yr^{-1} by Behrenfeld and Falkowski
484 (1997) and Carr et al. (2006) respectively. Zooplankton production as a fraction of primary
485 production was lower than in Yool et al. (2011) because of lower GGE (the
486 reparameterisation of AH95) and, because grazing on detritus was removed, predicted export
487 was higher in the new simulation (Table 2). The resulting export:PP of 0.18 is the same as in

488 Yool et al (2011), increasing only slightly to 0.19 and 0.20 for the simulations using the
489 ERSEM and HadOCC trophic transfer formulations.
490 Predicted primary production was ~10% higher in the AH95 simulation compared to that
491 using ERSEM (Fig. 7a; Table 1), higher than the 3% difference seen in the steady-state
492 model (for $\theta_P = 6.625$). Nutrient regeneration efficiency is the same for these two trophic
493 transfer formulations when phytoplankton are the food source (Table 1) and so the decrease
494 in primary production associated with ERSEM is due to the diminution in nutrient
495 regeneration resulting from mesozooplankton grazing on microzooplankton. The most
496 marked decreases are therefore seen in areas where mesozooplankton are most abundant
497 including the equatorial Pacific, North Atlantic and Southern Ocean. As was seen in the
498 steady state model, zooplankton production is closely linked to primary production and so
499 shows decreases in the ERSEM simulation similar to that of primary production (Fig. 7c).
500 The ZP:PP ratio remained at about 0.3 for each of the runs of the model. The predicted
501 pattern of zooplankton biomass (Fig. 7d) is, however, more complicated. Microzooplankton
502 account for approx. 60% of total grazing in each of the simulations and thus declining overall
503 zooplankton biomass is largely due to the impact of primary production on this group.
504 Mesozooplankton are compensated by having higher N GGE in ERSEM (relative to AH95)
505 because they consume a mixed diet that includes microzooplankton (Table 1) which led to
506 their biomass, and that of total zooplankton, increasing in some areas such as the Equatorial
507 Pacific. Predicted export was 10% lower in the ERSEM simulation due to lower primary
508 production, representing a weakened biological pump (Fig. 7e). The HadOCC model run
509 exhibited the lowest primary production (16% less than for AH95, with a similar change,
510 17% in the steady state model) as nutrient generation by zooplankton is only 6-13% of intake
511 (Table 1), with associated decreases in zooplankton production and stocks of phytoplankton
512 and zooplankton (Fig. 7a-d). The most interesting result is seen in the global distribution of

export predicted by the HadOCC model run. On the one hand, export decreases because of decreased primary production but, on the other, it increases in areas where diatoms are abundant because of the high allocation to fast-sinking faecal pellets (Table 1) that largely escape remineralisation in the upper water column. Overall, results show that relatively small changes in allocation of N intake to remineralisation or detritus (NGGE was the same in each case) gave rise to significant variation in predicted biogeochemical fields.

5. Discussion

When it comes to ecosystem modelling, it may be that even small changes in mathematical specification are amplified in model predictions (Wood and Thomas, 1999; Fussmann and Blasius, 2005). The implication is clear: accuracy is required in formulation and parameter values and, moreover, in the representation of the physico-chemical environment (Anderson, 2005). In a previous study focusing on zooplankton, Anderson et al. (2010) showed that the predicted distributions of plankton functional types in a biogeochemical GCM were sensitive to choice of functional response, a problem that is exacerbated by sensitivity to model physics and associated environmental forcing (Sinha et al., 2010). Here, we compared the performance of four contemporary trophic transfer formulations in two settings, a steady state food web model and a 3D biogeochemical GCM. The formulations differed in the way consumer growth was calculated as a function of food C:N ratio and in their assumptions for the fate of the non-limiting element. Results varied markedly for predictions of primary production, transfer to higher trophic levels and export, in both the steady state and 3D models.

At the outset, we should point out that our main priority is not to try and say which of the four chosen trophic transfer formulations is in some way the best, but rather to show that their disparate assumptions lead to contrasting biogeochemical simulations. In turn, this flags the

need for further investigation of the underlying assumptions, e.g., by comparing the different 3D simulations with global datasets for variables such as chlorophyll, primary production and nutrients, in order to see which showed the closest agreement. This is outside the scope of our work and, moreover, doing so would not have been a particularly meaningful exercise. For starters, parameter values used in the trophic transfer schemes were not tuned in any of the simulations which is arguably necessary in order to achieve an objective comparison. Without tuning, AH95 may have an unfair advantage because it was the formulation used in the MEDUSA ecosystem model as first published by Yool et al. (2011) and which forms the basis of our study. Further, even if we had undertaken parameter tuning, this is in itself problematic because the parameterisation of marine ecosystem models is often underdetermined by data (Ward at al., 2010). Errors elsewhere in the ecosystem model, such as those generated by physics, could confound conclusions drawn from a comparison of trophic transfer schemes in the 3D model.

5.1. Ecosystem dynamics and export

The predicted magnitude of regenerated production, and therefore primary production in total, varied between trophic transfer formulations depending on the extent to which N was regenerated by zooplankton excretion and so was highest for ERSEM and Pah08. Substantial errors may often occur in predicting primary production in GCMs, especially the gross underestimation seen in the oligotrophic subtropical gyres (Oschlies et al., 2000). One way to improve the match with data is to include an implicit microbial loop via a rapid recycling pathway from phytoplankton directly to inorganic nutrient (Doney et al., 1996) allowing primary production to be increased “by almost any factor desired” (Oschlies, 2001). Although such extreme variation was not the case here, predicted primary production did vary by as much as 10% in the 3D model depending on choice of trophic transfer scheme.

562 Predicted zooplankton production (ZP) is, unsurprisingly, sensitive to N GGE and how it
563 is parameterised. An interesting statistic, not often mentioned in modelling studies, is the
564 ratio of zooplankton production to primary production, ZP:PP (usually expressed in C units).
565 For θ_P = 6.625, predicted ZP:PP (for C) in the steady state model was 0.31 for the AH95
566 formulation and 0.35 for Pah03, ERSEM and HadOCC, decreasing at higher θ_P as N becomes
567 progressively limiting and C is in excess. Stock and Dunne (2010) estimated that
568 mesozooplankton production as a fraction of primary production, the *z*-ratio, varied between
569 0.01 and 0.04 in unproductive systems, increasing to between 0.1 and 0.2 when primary
570 productivity was high. Mesozooplankton such as copepods may however account for only a
571 relatively minor fraction phytoplankton grazing losses (e.g., 23%: Calbet, 2001). Rather, as
572 much as 59 to 75% of primary production may instead be consumed by microzooplankton
573 (Calbet and Landry, 2004). The *z*-ratio, as estimated by Stock and Dunne (2010), therefore
574 likely significantly underestimates total ZP:PP. In this context, one can argue that these two
575 zooplankton groups should be represented differently in models, taking into account the
576 physiological differences between organisms that phagocytose their food and those animals
577 with a gut (Mitra and Flynn, 2007).
578 Although herbivore growth was directly impacted by food quality, these zooplankton
579 prevented variability associated with phytoplankton C:N propagating up the food web in the
580 model because they are assumed to be homeostatic with respect to their body composition.
581 Theoretically, secondary consumers and higher trophic levels may thus be expected to be
582 unaffected by the stoichiometry of primary production, except via quantitative changes to
583 herbivore production (Brett, 1993; Boersma et al., 2009). If herbivores are predicted to be
584 limited by N, which occurs for $\theta_P > 5.5$ when using the ERSEM, HadOCC and Pah08 trophic
585 transfer formulations, their production is also independent of phytoplankton C:N and the
586 functioning of the food web depends only on N. In this case, food chain efficiency (FCE),

587 defined as the proportion of energy fixed by primary producers that is transferred to upper
588 trophic levels, decreases with increasing θ_P. These results highlight the importance of both
589 the assumption of homoeostasis and the need to understand how limiting factors associated
590 with food quality determine the growth of zooplankton (see section 5.2, below).
591 Export via sinking detritus also showed significant variation, depending on the choice of
592 trophic transfer formulation. Differences were minimal at low phytoplankton C:N, e.g. the
593 Redfield ratio of 6.625, in the steady state model. At high θ_P, however, carbon export was as
594 much as 50% higher when using the ERSEM and Pah08 formulations because these allocate
595 excess C to faecal pellets, as compared to AH95 where it is instead released as CO_2. The
596 predicted export of fast sinking detritus varied less because, being produced as carnivore
597 faecal pellets, stoichiometric variability associated with phytoplankton had been ironed out
598 by the herbivores. Predicted export varied by an average of almost 10% between the different
599 trophic transfer formulations in the 3D GCM, in this case for a fixed C:N in phytoplankton of
600 6.625. Regional variations were often greater, reflecting changes in both predicted primary
601 production and assumptions relating to zooplankton absorption efficiency.
602 *5.2. Stoichiometry in focus*
603 Although metazoans in general have a much tighter regulation of their elemental ratios
604 than autotrophs (Sterner and Elser 2002), the common model assumption that zooplankton
605 have fixed elemental ratios in biomass, i.e., exhibit homeostasis, is nevertheless open to
606 question. While many experimental studies using nutrient limited algae have demonstrated
607 grazer deviations from homeostasis, secondary consumers may also experience such
608 deviations, especially with regard to C:P (Dickman et al., 2008; Malzahn et al., 2010; Schoo
609 et al., 2010). Seasonal changes in C and N content are known to occur in copepods from high
610 latitudes due to lipid accumulation (Tande, 1982; Donnelly et al., 1994), largely reflecting
611 ontogenetic differences in lipid sequestration and catabolism (Kattner and Krause, 1987;

612 Kattner et al., 1994; Mayzaud et al., 2011). Indeed, it may be that at high latitude,
613 overwintering copepods should be considered as two-compartment systems in a
614 stoichiometric context, with lipids sacs (consisting mostly of wax esters) and somatic tissue
615 as separate entities.

616 Homoeostasis aside, the limitation of zooplankton production remains incompletely
617 understood. The question "carbon or nitrogen limitation of marine copepods?" was asked
618 more than 15 years ago by Anderson and Hessen (1995) yet, despite advances in
619 experimental ecology and stoichiometric theory, it remains to be comprehensively answered.
620 There is now a greater appreciation of the roles of many factors in zooplankton nutrition and
621 stoichiometric balance including the potential for limitation by fatty acids and other
622 micronutrients (Anderson and Pond, 2000; Anderson et al., 2004), nutrient element
623 requirements for maintenance (Boersma and Kreutzer, 2002; Mayor et al., 2011), the
624 potential for maternal biomass to fuel production (Mayor et al., 2009a,b) and the influence of
625 gut residence time (Thor and Wendt, 2010) and biochemical composition (Reinfelder and
626 Fisher, 1991; Anderson, 1994; Mayor et al., 2011) in determining absorption efficiencies.
627 Providing reliable equations to calculate zooplankton production on the basis of these factors
628 is an ongoing challenge for modellers. In particular, the whole concept of Liebig-style
629 limitation of zooplankton production is open to scrutiny, an alternative approach being, for
630 example, the use of Dynamic Energy Budget theory in which different reaction pathways
631 using C and N proceed on a probabilistic basis using synthesising units (Kuijper et al., 2004).

632 The various trophic transfer schemes investigated here involve different choices regarding
633 whether stoichiometric regulation occurs pre-or post-absorption by the gut, which has
634 particular biogeochemical implications for whether organic matter is recycled in inorganic
635 form in the upper ocean, or exported to depth as sinking detritus. If one consults the
636 contemporary literature on plankton physiology, there would appear to be little exact

637 knowledge on the mechanisms of stoichiometric regulation in metazoans (Hessen and
638 Anderson, 2008). Anderson et al. (2005) proposed that, although digestive plasticity allows
639 some flexibility for consumers to regulate stoichiometric balance in response to shifts in diet
640 quality, especially long term variations, generalist consumers should employ post-absorptive
641 regulation as an effective means of dealing with short term variations in food quality. In
642 theory, this allows animals to effectively monitor available substrates, in the same way that
643 hormonal systems operate in higher animals. Experimental studies have provided evidence of
644 disposal of excess C as dissolved organic material (Darchambeau et al., 2003) or as
645 respiration to CO_2 (Jensen et al., 2006; Jensen and Hessen, 2007). Yet, others have provided
646 evidence for defecation of C-rich compounds by zooplankton via enzymatic discrimination in
647 the gut (DeMott et al., 1998) which may be a useful strategy if food items follow predictable,
648 e.g. seasonal, changes in food quality. Matters are complicated further by the interaction
649 between food quality and quantity, the effects of which are often mutually at odds with each
650 other, with important trophic implications (Mitra and Flynn, 2007; Flynn, 2009).

651 *5.3. Adequacy of existing parameterisations*

652 What are we to conclude about the suitability of the different trophic transfer schemes
653 investigated herein for use in marine ecosystem models? Any or all of them can be readily
654 criticised with regard to their underlying assumptions. None take into account the effect of
655 food quantity on absorption efficiency, nor biochemical aspects of nutrition (although the
656 originally published version of AH95 did separate C between protein and
657 lipids/carbohydrates and specify separate AEs for each). The ERSEM, HadOCC and Pah08
658 formulations each make the apparently simplistic assumption that the ideal food C:N equals
659 that of consumer biomass, arguably without a full appreciation of metabolic requirements
660 (although it should be noted that, as parameterised, they do a reasonable job at reproducing
661 the data set of Kiørboe (1989) shown in Fig. 3). It is also possible to question the efficacy of

662 calculating growth Liebig-style based on empirical gross growth efficiency parameters.
663 Regarding the fate of non-limiting substrates, there was no consensus as to whether
664 stoichiometric regulation of C and N in excess should be pre-or post-absorption by the gut, an
665 important decision because it impacts on predicted nutrient recycling and export. Matters are
666 not improved by the fact that, in the published originals, little or no justification is generally
667 provided for the various assumptions that were made.

668 The fact that the assumptions in the four trophic transfer schemes were so disparate
669 suggests a lack of consensus within the scientific community as to how trophic transfer is to
670 be modelled. The implication is that more information is needed on the nutritional factors
671 controlling growth efficiency in consumers, stoichiometric regulation of homoeostasis (e.g.,
672 pre-versus post-absorptive), the fate of substrates in stoichiometric excess, absorption
673 efficiency, and the metabolic budgets of zooplankton, especially the factors contributing to
674 maintenance. Improved estimates of processes such as protein turnover, and other metabolic
675 costs, are required (Mayor et al., 2011).

676 On the other hand, it is easy for modellers to deflect attention from model deficiencies by
677 pointing to insufficient information or understanding on key processes or organisms.
678 Scientists live today in a hustle bustle, publish or perish society. Everyone is pressed for time
679 and ignorance (e.g. because of lack of time to familiarise with the latest literature) and
680 indifference (lack of interest) are easy traps for modellers, as well as other scientists, to fall
681 into (Anderson and Mitra, 2010). As the English poet Thomas Gray said, “Where ignorance
682 is bliss, ‘tis folly to be wise” (i.e., what you do not know cannot hurt you). In moderation, we
683 should note that it is nigh impossible to keep on top of the ever-growing mountain of
684 literature that confronts scientists today. This is especially so if numerous disciplines are to
685 be covered, as is often the case for modellers, highlighting the need to initiate and/or maintain
686 genuine, active dialogue between the modelling and observational/experimental communities

687 (Flynn, 2005). Another problem is inertia since, once a model is operational and published,
688 modellers often remain faithful to that version regardless of changes to our understanding.
689 Revisiting equations is potentially awkward since it changes the model from its original,
690 citable form and may also require a retuning exercise which can, as when using GCMs, be
691 prohibitively costly in time and effort. It is thus easy to see how multiple factors conspire to
692 allow outdated formulations to be retained in ecosystem models. Our aim here is to raise
693 awareness of these potential pitfalls.

694 Advanced parameterisations of trophic transfer, beyond the formulations investigated here,
695 have been developed in recent years, although have not as yet been implemented within
696 GCMs. Anderson et al (2005) developed a model of trophic transfer which did away with the
697 empirical gross growth efficiency parameters, replacing them with a detailed description of
698 the costs of maintenance and growth, with C-rich substrates preferentially utilised thereby
699 sparing N in proteins for growth. Mitra (2006) also developed an advanced parameterisation
700 where respiration included separate terms for basal metabolism (maintenance of osmotic and
701 ionic gradients, enzyme turnover and DNA repair) and metabolism (including synthesis of
702 new biomass). Zooplankton growth is calculated as ingestion minus respiration and voiding
703 to faeces, with excess substrates incorporated primarily into the latter. We chose not to
704 include these transfer schemes in the analysis presented here because they represent basal
705 metabolic costs of consumers in a completely different way, preventing a consistent approach
706 for the comparison (see section 2). If metabolic costs are equalised, the Anderson et al.
707 (2005) trophic transfer scheme exactly reduces to AH95. Our comparison of trophic transfer
708 schemes focused on assumptions relating to the calculation of growth and on the fate of non-
709 limiting substrates. A further point for consideration by modellers is the specification of
710 energetic costs associated with basal metabolism and growth. In aspects other than the
711 explicit calculation of maintenance and bioenergetic costs, for which parameter values such

712 as protein turnover are often hard to come by (Mayor et al., 2011), the Anderson et al. (2005)
713 and Mitra (2006) formulations are remarkably similar to AH95, ERSEM, HadOCC and
714 Pah08 in that they make simple assumptions for Liebig-style limitation of production and as
715 to whether excess C and N is respired/excreted post-absorption by the gut. For organisms
716 with a gut, there is an important linkage between absorption of food and gut transit time
717 (Paffenhöfer and Van Sant, 1985; Tirelli and Mayzaud, 2005). By including this, the model
718 of Mitra and Flynn (2007) represents a significant departure from other formulations of
719 trophic transfer which has the potential to significantly change the dynamics of the whole
720 system through a process of density dependent inefficiency (Mitra and Flynn 2007; Flynn,
721 2009). The extra complexity associated with these trophic transfer schemes brings problems
722 with assigning suitable parameter values, a common issue with increasing complexity in
723 models. They should be used to help in the formulation of simpler model structures that are
724 amenable for placement in ecosystem models.

725 *5.4. Concluding remarks*

726 Worrying inconsistencies are evident in the way in which fundamental transfer processes
727 are justified and parameterised in the current generation of marine ecosystem models. Our
728 results using a simple steady state model and a 3D GCM showed that this lack of conformity
729 manifested itself in the simulation of ocean biogeochemistry, notably primary production,
730 transfer to higher trophic levels and export. As a result, “one wonders ... to what extent the
731 parameterisations used in the current generation of complex ecosystem models being
732 developed for climate studies, and the predictions thereof, can be relied upon” (Anderson and
733 Mitra, 2010). Identifying the most appropriate formulations for use in ecosystem models is,
734 however, no easy matter. We made no attempt to do so on the basis of comparing our 3D
735 simulations to see which agreed most closely with data, because of the problem of
736 underdetermination (Ward et al., 2010). This does not mean, however, that the

parameterisation of ecosystem models, including those for use in global GCMs, is a forlorn task. Parameter tuning and investigation can instead be undertaken for local, data-rich domains such as the various time series stations that adorn the world oceans. Equally important is for modellers to ensure that the component parts of their models are parameterised individually to the highest standards on the basis of known physiology. Local inadequacies in the equations and parameterisation need to be identified and related to underlying assumptions. Only then can "piecemeal engineering" (Simon, 1996) be carried out to modify the offending parts.

Overall, our work has highlighted serious deficiencies in the way in which trophic transfer is parameterised in contemporary marine ecosystem models. It demonstrates the need for modellers to adopt a back to basics approach and revisit some of the basic assumptions used in the formulation of zooplankton, involving active dialogue between modellers and the observational/experimental community. It will of course also require consideration of the usual trade-off between simplicity for the sake of pragmatic parameterisation, and complexity to achieve the desired basis in reality. If the underlying physiology in models is not afforded due attention, then it may be that our models are like "castles built on sand" (Flynn, 2005).

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1028

1029 **Figure Legends**

1030 Figure 1. Flow pathways of the 4 trophic transfer schemes. Ingested food (I) is allocated to
1031 zooplankton biomass (Z), faecal material (detritus: D), dissolved organic matter (DOM), CO_2
1032 and inorganic N (NH_4). C flows unshaded, N flows shaded. Release of substrates in
1033 stoichiometric excess is shown in hexagons.

1034 Figure 2. Comparison of allocation schemes for the AH95, ERSEM, HadOCC and Pah08
1035 trophic transfer formulations: predicted allocation of a) N and b) C in ingested food between
1036 growth (black), faecal pellets (grey) and excretion/respiration (stippled), for food C:N
1037 varying between 4 and 20.

1038 Figure 3. Comparison of predicted gross growth efficiencies for a) N and b) C using the
1039 AH95 and ERSEM trophic transfer formulations with the experimental data for the copepod
1040 *Acartia tonsa* feeding on the diatom *Thalassiosira weissflogii* (Kiørboe, 1989).

1041 Figure 4. Flow diagram of the steady state model showing how new (Pn) and regenerated (Pr)
1042 production by phytoplankton (P), consuming nitrate (N) and ammonium (A) respectively, is
1043 cycled via herbivores (H) and an infinite chain of carnivores (Z), leading to export (Ex) via
1044 slow- and fast-sinking detritus (D_1 and D_2).

1045 Figure 5. Solutions of the steady state model, for θ_P between 4 and 20, in each case to
1046 normalised to P_n: a) primary production (P_n+P_r), b) herbivore production (G_H), c) carnivore
1047 production (G_Z), d) C export via fraction D_1 ($Ex_{D1(C)}$), e) C export via fraction D_2 ($Ex_{D2(C)}$), f)
1048 C:N of export (given that P_n=1, this equals total export, $Ex_{D1(C)}$+$Ex_{D2(C)}$).

1049 Figure 6. Flow diagram of the MEDUSA ecosystem model (Yool et al., 2011).

1050 Figure 7. Comparison of simulated biogeochemical fields in MEDUSA-NEMO for the
1051 different trophic transfer formulations. Predicted values shown for AH95 and the absolute
1052 difference from AH95 for ERSEM/Pah08 and HadOCC.

1053